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Abstract

In order to stop the continuous decline of typical dune slack communities along the Dutch coast, restoration projects have been carried out since 1952. Restoration measures consisted of re-introducing traditional management techniques in dune slacks, such as mowing, grazing and sod removal, or constructing artificial dune slacks to compensate for lost biodiversity elsewhere. An analysis of successful and unsuccessful projects showed that constructing new dune slacks was not very successful for maintaining new populations of endangered dune slack species, since such projects were often carried out in areas where seed banks were depleted, while hydrological conditions and seed dispersal mechanisms were sub-optimal. The construction of sand dikes to prevent sea intrusion in large beach plains was, unintentionally, a temporary success for the establishment of many Red List species, although such measures often disrupted natural dune slack formation. Successful sites were all characterised by a regular discharge of calcareous groundwater provided by local or regional hydrological systems, where not very long ago populations of typical dune slack plants were present. Under such conditions, sod removal was a successful measure to create pioneer stages which were relatively stable, due to a very slow accumulation of organic matter in the topsoil. It is argued that new and more flexible coastal defence strategies can provide new opportunities for natural and relatively stable pioneer stages of dune slack formation, suitable for the long term preservation of endangered dune slack species.

Introduction

Coastal dune areas represent one of the last nutrient-poor landscapes in The Netherlands (Fig. 1) and are characterised by pronounced geomorphological and hydrological gradients, thus creating good conditions for a high biodiversity of plants and animals. Most of the species featuring on the Dutch Red List of endangered plant species now have their main distribution in the coastal area, but few are real endemic species (van der Maarel & van der Maarel-Versluys, 1996). Most species are restricted to the dune areas because practically all their main land populations have become extinct due to severe drainage, acidification and eutrophication. Pioneer communities, in particular, are rich in Red List species. The last four decades, however, have shown a steep decline in typical dune slack vegetation, especially along the Holland coast, due to intensive use of that area for the production of drinking water. This decline has triggered numerous activities to restore the species-rich dune slack stages with many Red List species. Sometimes such activities were successful, but more often success was limited. An interesting phenomenon is, though, that some human activities in the framework of coastal defence, unintentionally triggered the development of pioneer dune slack stages with many Red List species.

On order to provide dune managers with a good blue-print for successful dune slack restoration we have studied some 50 projects and selected 12 that had been monitored in a systematic way for at least six years. In the present paper, we will evaluate the

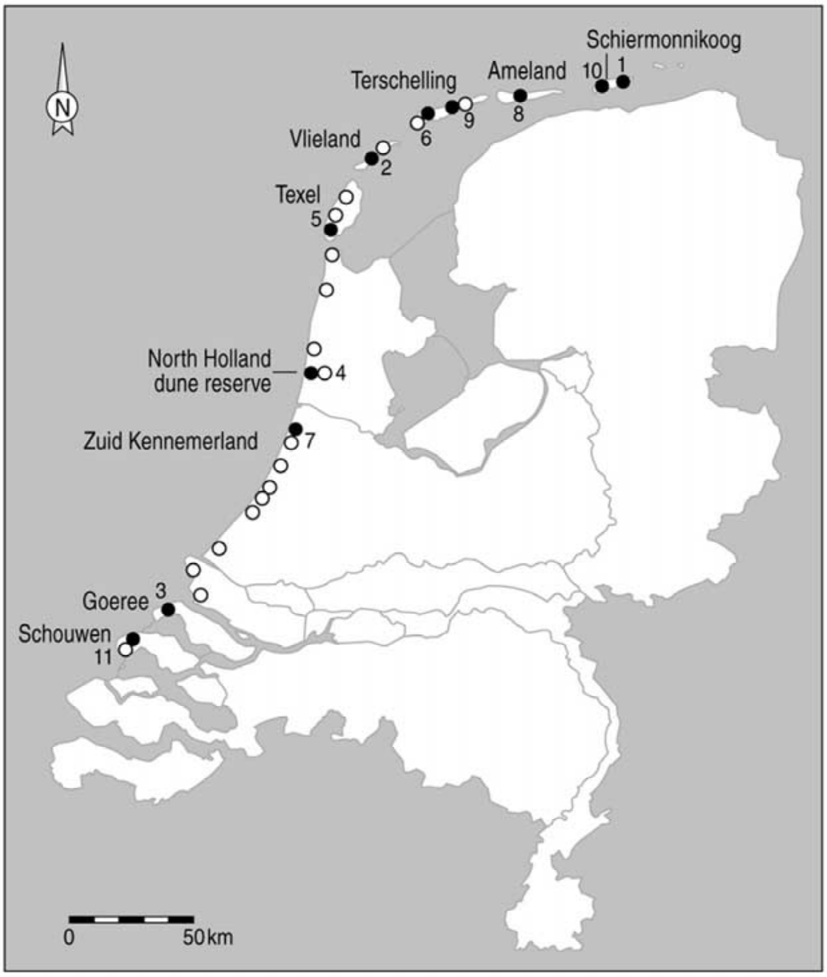

Figure 1. Dune areas in The Netherlands with position of the research areas. 1 = Beach Plain Schiermonnikoog, 2 = Kroon's Polder Vlieland, 3 = Middelduinen Goeree, 4 = Reggers Sandervlak, 5 = Moksloot Texel, 6 = Hunenplak Terschelling, 7 = Vogelmeer Kennemerduinen, 8 = Lange Duinen Ameland, 9 = Koegelwieck Terschelling, 10 = Kapenglop Schiermonnikoog, 11 = Vroongronden Schouwen.

successes and failures of these restoration projects and use the number of re-established Red List species to judge their success. The analysis is preceded by a short review on the structure and functioning of dune slacks, the ecological and hydrological requirements of dune slack species, and various (human) disturbances in dune slack functioning. Measures to restore acidified or eutrophicated dune slacks will be shortly discussed and successful and less successful projects assessed. Finally, the state of the art of dune slack restoration will be summarised in a conceptual model.

Structure and functioning of dune slacks

Site factors and plant adaptations

Dune slacks are low-lying areas within the coastal dunes where high water tables prevail during winter and spring (van der Laan, 1979; Boorman et al., 1997; Grootjans et al., 1998). During the summer period the water table may drop 50–100 cm below the surface. Young dune slacks are very nutrient poor but show a large variability with respect to species composition, depending on their substrate characteristics and hydrological regime. Figure 2 shows the results of a canonical correspondence analysis (CCA), relating the occurrence of plant communities from 51 sites on the Dutch Wadden Sea islands with measured en-

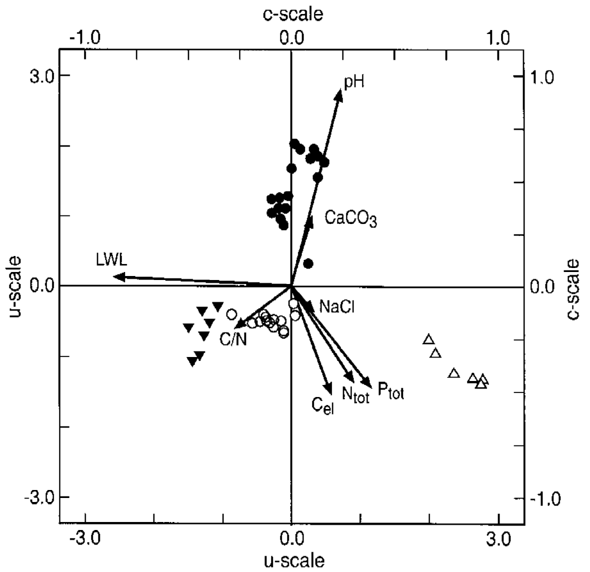

Figure 2. Results of Canonical correspondence analysis (CCA) showing the relationships between measured environmental factors (0–10 cm) and species composition in dune slacks on the Dutch Wadden Sea islands (from Lammerts & Grootjans, 1999). LWL = mean lowest water level, C_{el} = carbon content, N_{tot} = total nitrogen content, P_{tot} = total phosphorus content.

vironmental factors (Lammerts & Grootjans, 1998). The length of the arrows corresponds with the magnitude of greatest variation in the total data set. In this analysis, the mean lowest water level and the pH are the factors explaining most of the variation in species composition. The occurrence of the typical dune slack community is clearly related to sites with a relatively high pH and intermediate soil moisture conditions. Late successional stages, such as eutrophic reeds and small sedge marshes occur at less calcareous sites with higher soil nutrient stocks (N-total, P-total). Due to nutrient-poor conditions the vegetation cover of pioneer communities is low. Young slacks consist of a mixture of different life and growth forms: annuals, biennials, perennials, young shrubs and trees (Crawford & Wishart, 1966; Ranwell, 1972). Older slacks may be completely covered with shrubs and trees when natural succession has taken place. Nutrient stocks are high, both in the vegetation and in the shallow organic soil layer. The Dutch coast has an Atlantic climate where precipitation dominates over evaporation. This leads to prominent decalcification processes in the top layer and to rapid acidification in areas with a low initial lime content, as is the case in the Wadden Sea area (less than 2% $CaCO_3$).

Most typical dune slack species have to cope with hydrological very dynamic conditions. Anoxia tolerance is one of the dominant factors responsible for a stable vegetation within the dune slack (Studer-Ehrensberger et al., 1993). A very critical factor is the height and the length of the winter flooding. Plant species with well-developed aerenchyma such as *Schoenus nigricans*, *Littorella uniflora* can counteract the deprivation of oxygen from the soil by high levels of radial oxygen loss (ROL). They can survive as mature plants when flooded as long as a small part of the shoot can keep in contact with the atmosphere (Armstrong, 1975). Anoxic conditions, therefore, may prevent the establishment of late-successional species without ROL capabilities since they enhance the supply of reduced iron and manganese and also sulphide. Sulphide in particular can be very harmful for plant species if it remains in a reduced state. In addition to anoxia, dune slack species have to cope with nutrient-poor conditions (Schat et al., 1984). Many species, such as *Littorella uniflora, Centaurium pulchellum*, and *Radiola linoides*, have a very low nutrient demand because they are very small. Others, such as *Schoenus nigricans*, are long-lived tussocks forming species with a diameter of up to 35 cm and a height of over 70 cm. *Schoenus* has a very efficient recycling of nitrogen and phosphorus from senescent to juvenile leaf and shoot tissue (Ernst & van der Ham, 1988). In this way, they can capture much nutrients in the tussock making them unavailable for fast growing herbaceous species and later successional grasses such as *Calamagrostis epigejos*.

Types of dune slacks

Two types of dune slacks can be distinguished on the basis of their geomorphological history; primary and secondary slacks (Boorman et al., 1997). Primary slacks originate from sandy beaches, which have been partially or fully cut off from the influence of the sea. The soil in young primary slacks can be buffered by any combination of brackish surface water, $CaCO_3$-rich sand, and calcareous groundwater. Secondary slacks result from blowouts. They are usually calcareous and may or may not be supplied by calcareous groundwater. In both cases, the vegetation may be very similar since infiltration of rainwater also leads to base-rich conditions, since $CaCO_3$ is dissolved in the rooting zone almost immediately. Secondary, *in situ*, carbonate deposition has also been observed in dune slacks. It occurs when exfiltrating

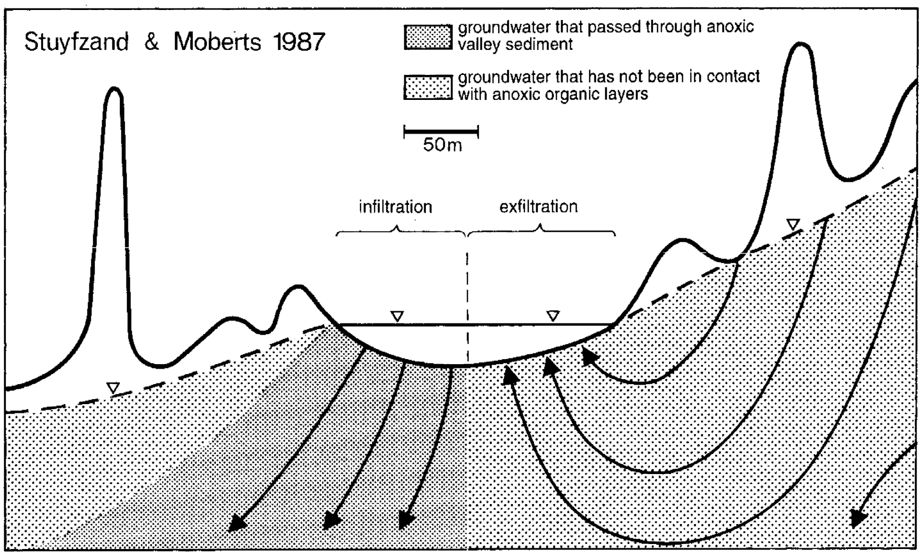

Figure 3. Groundwater flow pattern in a cross section through a dune slack with high water levels in the upper part of the dune area and low water levels close to the sea. Groundwater exfiltrates at the upgradient side of the slack and infiltrates at the opposite site, but only when the slack is flooded (after Stuyfzand & Moberts, 1987).

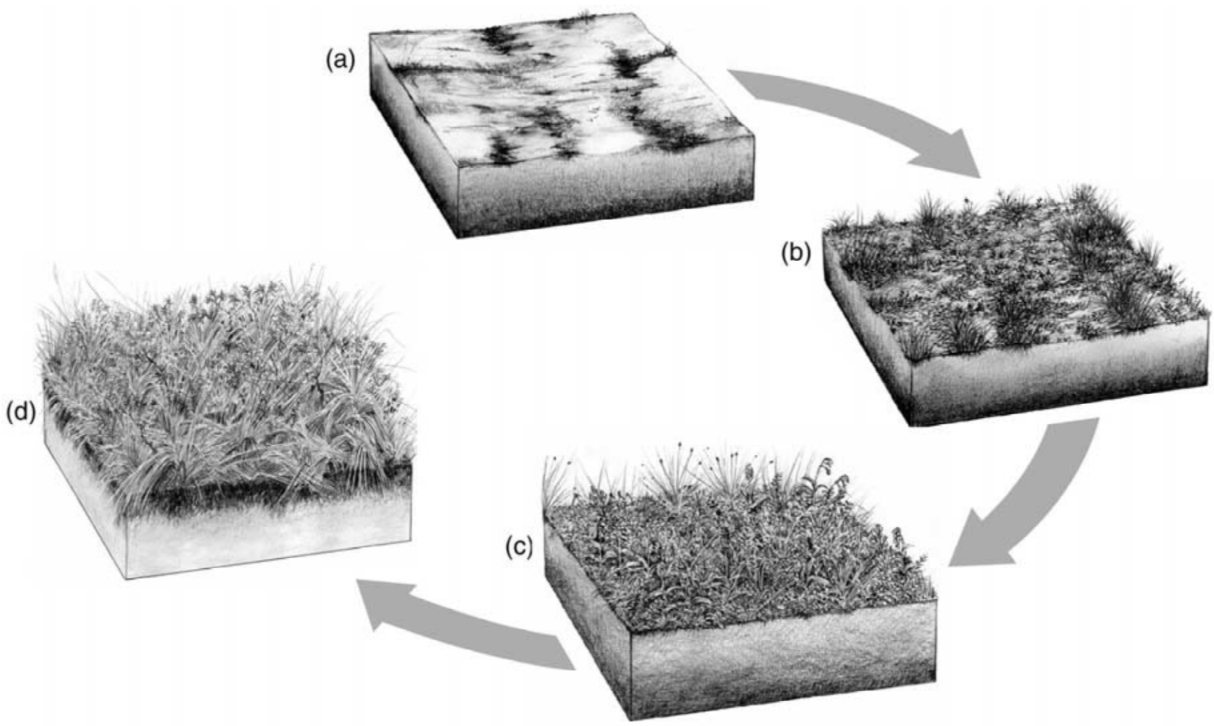

Figure 4. Vegetation development in a wet dune slack starting as sparsely vegetated pioneer stages (a and b), proceeding to a stage with many Red List species (c), until tall grasses and shrubs (d) take over (drawing by Rob Beentjes).

groundwater, (over) saturated with respect to calcite, enters the slack. Loss of CO_2 from this water results in carbonate precipitation at the soil–air interface (Krauskopf, 1982; Chafetz, 1994), thus counteracting soil acidification in a very significant way. Such carbonate precipitation can only occur when water tables remain very high during summer (c. 40 cm below the surface) and capillary rise of calcareous groundwater is possible.

Slacks in decalcified areas can harbour basiphilous vegetation types only if they are supplied by calcareous groundwater from surrounding dune areas. The best examples are situated at the low-lying periphery of the dune system, where most of the groundwater of the main hydrological system discharges. However, seepage slacks can also be found close to the top of the main hydrological system when thick clay or peat layers prevent infiltration to deeper layers and give rise to local groundwater flow towards adjoining dune slacks. Such slacks function as 'flow-through lakes' with groundwater discharge in one part of the slack and infiltration of surface water in another (Fig. 3). This hydrological mechanism can only function during the time that the slack is flooded and when high water tables in the surroundings occur (Stuyfzand & Moberts, 1987; Grootjans et al., 1996). Under such conditions, calcareous groundwater from deeper layers can flow towards the upgradient parts of the slack. The influx of calcareous groundwater stimulates mineralisation of organic matter and consequently the accumulation of organic matter is lower here than at the infiltration sites (Sival & Grootjans, 1996).

Succession

Natural succession in dune slacks can be roughly divided into 4 phases (Fig. 4): a pioneer phase (phase 1) in which small pioneer species establish on an almost bare soil, which is usually covered with a thin layer of green algae and laminated microbial mats (van Gemerden, 1993; Grootjans et al., 1997), (phase 2) colonisation of phanerogams adapted to very low nutrient availability, (phase 3) development of a moss layer of pleurocarpic bryophytes and establishment of typical dune slack species, and on older phase (phase 4) in which rapid accumulation of organic matter and increase of tall grasses and shrubs appears, which leads to the decline of typical dune slack species. The microbial mat in phase 1 stabilises the sandy substrate (Pluis & de Winder, 1990). The Cyanobacteria in the microbial mats can fix nitrogen (Stal et al., 1994) and may, therefore, assist in the colonisation by phanerogams. The dense layer of pleurocarpic bryophytes in phase 3 promotes the rapid built up of organic material and the establishment of tall grass and willow species. These eventually form a dense vegetation cover which prevent light penetration through the dense canopy, leaving little space for small dune slack species. Red list species are most abundant in phase 2 and 3. Orchids only occur in these early successional stages, where they receive nutrients from soil mycorrhizas (Smith, 1966). Juvenile orchids in particular are almost totally dependent on nutrients from mycorrhizas.

Succession along most of the Holland and Zeeland coast differs from that on the Wadden sea islands, because the initial lime content is higher (Fig. 1). Decalcification in the topsoil, therefore, begins in early stages of succession on the Wadden Sea islands. Furthermore, primary dune slacks on the Wadden Sea islands are often flooded by brackish surface water, which is a rare phenomenon along the Holland and Delta coasts.

Stability of pioneer stages

Large differences in the stability of the pioneer phase have been observed in dune slack succession (Lammerts & Grootjans, 1995). Micro-organisms and algae may contribute to the stability of the pioneer stage of dune slacks. They can form so-called microbial mats (van Gemerden, 1993) which are most abundant in tidal flats and salt marshes, but occur also in pioneer stages of dune slacks. Recent research suggests that in some fresh water dune slacks microbial mats may assist in retarding the natural vegetation succession (Grootjans et al., 1997), thus extending the life span of pioneer stages. The shift from pioneer stage to more mature stages usually takes place between 20 and 30 years (van der Maarel et al., 1985). In some dune slacks, however, pioneer stages may last for at least 30–60 years (Sival & Grootjans, 1996: Peterson, 2000). The succession rate and soil development in dune slacks is largely controlled by the productivity of the ecosystem, decomposition of organic matter and recycling of nutrients within the ecosystem (Koerselman, 1992; Verhoeven et al., 1996). The low productivity during the first years of vegetation development in dune slacks is the main cause of the low content of organic matter and the slow succession rate. The high hydrological dynamics may stimulate a rapid mineralisation of organic matter, especially under alkaline conditions. Tussock forming species as *Schoenus nigricans* can modify their environment by retention of nutrients in living and dead biomass, resulting in spatial aggregation of nutrients.

Fertilisation experiments in different chronosequential stages, originating from sod cutting at different times intervals, showed that late successional grass species, such as *Calamagrostis epigejos* and *Agrostis stolonifera*, are already present in pioneer stages, but that their growth was limited by a low availability of both nitrogen *and* phosphorus (Ernst et al., 1996; Lammerts et al., 1999). The low productive pioneer species, in particular *Juncus* and *Carex* species, were only nitrogen limited (Lammerts & Grootjans, 1997), most likely because they have a very low phosphorus demand (Willis, 1963; van Beckhoven, 1995). *Schoenus nigricans* showed no response at all to either nitrogen or phosphorus additions. This implies that, as long as phosphorus limits the growth of tall grasses, a basiphilous pioneer vegetation can persist for quite some time, even when nitrogen availability increases. Buffer mechanisms that keep the soil pH above 6, appear to be crucial for maintaining a low phosphorus availability. Adding lime in the fertilisation experiments had the same effect on biomass production as the effects of co-limitation by nitrogen and phosphorus.

Atmospheric input of nitrogen may accelerate the accumulation of organic matter in the topsoil considerably, because the growth of most pioneer and mid-successional species is N-limited and, therefore, responsive to additional supply of nitrogen.

Summarising, the hydrological regime of a dune slack is essential for a good functioning of the dune slack ecosystem. Factors that stabilise the longevity of pioneer stages comprising many Red List species are always associated with a regular supply of groundwater.

Disturbances in ecosystem functioning

Large scale disturbances of dune slack environment along the Holland coast in particular started around 1853 when the vast stock of fresh dune water became a major source of drinking water production for the large cities. Large dune areas actually became drinking water catchments. The exploitation of dune water resulted in a large scale lowering of the water table by 2–3 m on average (Bakker & Stuyfzand, 1993). At the same time, large parts of the dune area were saved as a landscape in a time of rapid industrialisation and rapid urbanisation in this densely populated area.

Factors that contributed to the dramatic decline of wet dune slacks along the Holland coast during the second half of the century were lowering of the water levels in the adjacent polder areas, reclamation for agricultural use and afforestation with pine plantations (see Janssen & Salman, 1995 for an overview). In a later stage, a new drinking water production technique was developed: infiltration of surface water from the rivers Rhine and Meuse. This input of polluted river water led to increased water tables in the dune slacks, but at the same time promoted eutrophication (van Dijk et al., 1985; van Dijk & Grootjans, 1991). In some areas, desiccated dune slacks were used as infiltration ponds, in others new infiltration ponds were excavated in the dune area.

In less affected dune areas, as the Wadden Sea coast, 70 years of dune fixation, in which every spot of bare soil was covered with branches or hay, resulted in an almost complete stop in natural dune formation. This has led to ongoing succession, which was accelerated by atmospheric deposition from industrial areas. The total amount of atmospheric N-deposition has increased between 1930 and 1980 from c. 10 kg N ha^{-1} yr^{-1} to c.25 kg N ha^{-1} yr^{-1} (Stuyfzand, 1993) and has stabilised between 25 and 35 kg N ha^{-1} yr^{-1}in the late 1990s (ten Harkel & van der Meulen, 1996; van Wijnen, 1999).

Decreased grazing by cattle and rabbits also enhanced grass encroachment (Veer, 1997) and the development of woodland. A positive feedback mechanism exists between increased biomass production and decreased groundwater availability. Tall vegetation types, such as shrubs and forests intercept more nutrients from atmospheric deposition than relatively open and short vegetation types, which leads to increased growth and a higher evapotranspiration. The result is an increased drop in water tables during the summer and consequently in a decreased discharge of groundwater in the dune slacks (Stuyfzand, 1993). If the supply of groundwater decreases, shrubs and tall grass species invade the site and pioneer communities lose the competition due to increased availability of nutrients.

A future threat to wet dune ecosystems could be caused by predicted sea level rise due to overall changes in climatic conditions. Sea level rise as a consequence of global warming could either lead to a drop or a rise in the phreatic water level, depending on erosion and accretion rates along the coastline (Noest, 1991).

Restoration of dune slacks; why and how?

Nature conservancy tries to stop the decline of pioneer communities by initiating restoration projects. The aim is to restore or stabilise pioneer stages of dune slack succession in order to provide endangered plant and animal species with habitats where their required site conditions are sustained for a long time. Dune slacks harbour many endangered fen species which have become almost extinct in mires on the mainland in most of Western Europe. Dune slacks, therefore, are listed high on the international conservation agenda. Restoration of dune slacks is relatively easy compared to restoration of mires. The restoration of fen ecosystems, for instance, usually requires a complete reconstruction of large hydrological systems (Pfadenhauer & Grootjans, 1999). In young dune slacks, the pool of stored nutrients is still small compared to the large peat deposits in fens. Consequently dune slack release less nutrients to the environment when changes occur in the hydrology.

The aim, therefore, is to create nutrient-poor, open and wet conditions that remain more or less stable for some decades. Most nature conservation organisations realise that the best option for continuous rejuvenation of dune slack ecosystems is to allow natural dune forming processes to take their course (Janssen, 1995). Encouraging these natural processes is, however, often blocked by established forms of land use in dune areas: sea defence, tourism, housing, forestry, production of drinking water etc.

The following management techniques have been applied in Dutch dune slacks to combat the negative effects of acidification, eutrophication and desiccation: (i) mowing, (ii) grazing, (iii) rewetting (iv) sod-cutting, and (v) creating new slacks.

Mowing

Mowing is a traditional management technique, which when applied without addition of fertiliser or manure, prevents grasses, willows and tree species to dominate the vegetation, thus favouring many non-competitive Red List species. The production of dead biomass is less because part of the biomass is harvested. This leads to decreased nutrient cycling within the ecosystem and might even lead to a shift in the type of nutrient limitation (Koerselman et al., 1995; Verhoeven et al., 1996). Mowing does not prevent the accumulation of organic matter in the top layer and it does not prevent acidification in decalcified soils. Mowing, therefore, is most efficient in sustaining basiphilous pioneer stages in areas where the soil is well buffered against acidification and where nutrient cycling is still low; in calcareous dune soils and in soils with a strong discharge of calcareous groundwater. Mowing early in the season can be very harmful, because it affects reallocation of nutrients in *Schoenus* tussocks and prevents seed set (Ernst, 1991).

Grazing

Grazing is often applied in dry dunes to combat grass and shrub encroachment. In wet dune slacks, cattle and horses may damage young pioneer stages by trampling and by polluting surface water. The effect of grazing by rabbits is most pronounced in early stages of succession. They may eat 40–50% of the shoot biomass during the first three years after sod cutting (unpublished data from van der Veen). Accumulation of organic matter is not prevented by grazing, but perhaps retarded, due to a lower input of litter (Kooijman & de Haan, 1995). Species-richness is locally stimulated by cattle grazing and some dominant species, such as *Calamagrostis epigejos, Salix repens* and *Carex arenaria* decrease in cover (van Dijk, 1992; Annema & Jansen, 1998; de Bonte et al., 1999). In general, grazing promotes low structured vegetation types and creates a more fine-grained vegetation pattern. In Moksloot area cattle reduced tall reeds and tall sedges including rare species such as *Ranunculus lingua*, leaving a monoculture of *Iris pseudacorus*

Rewetting

At present, adaptations in the hydrological system are applied frequently to rise water tables in dune areas. The extraction of natural dune water is further reduced. In the National Park of 'Zuid Kennemerland', for instance, existing groundwater extraction (9 Mm^3 a year) was eliminated. A large production canal of 2.5 km has been eliminated in the dunes near Amsterdam, leading to a spectacular rise in water tables of 2 m. Rewetting was combined with a restoration project of the whole dune landscape. (Geelen et al., 1995). In the near future, the elimination of groundwater extraction will lead to further rewetting of hundreds of hectares of desiccated dune slacks. In the Meyendel area, a production field with surface infiltration was recently removed to restore the hydrological system. This termination of production fields became possible due to the development of new production techniques, such as deep-well infiltration and membrane filtration (Janssen & Salman, 1995). Further adaptation in local hydrological systems includes the rising of water tables by closing drainage ditches and hydrological isolation of low lying polders by placing artificial shields in the soil to prevent loss of groundwater.

To restore species-rich dune slacks, rewetting of desiccated slacks has to be combined with one of the management techniques mentioned. Otherwise grasses, tall herbs and shrubs will soon dominate the vegetation.

Sod cutting

Sod cutting includes the removal of the black organic A-horizon and leaving the mineral C-horizon intact. This type of management is traditional and has been practised (manually) on most of the Dutch, German and Danish coastal dune areas for a long time (Peterson, 2000). Nowadays sod removal is often carried out with large machines and affects sections of the mineral subsoil as well. In many restoration projects, the dune slack is deepened on purpose, to promote rewetting of the slack. This approach of combining decreasing nutrient stocks with rewetting is applied on a large scale in Dutch dune areas, but deviates from natural dune slack formation in several ways. Firstly, large-scale sod cutting is carried out within a very short time, usually in summer, when water levels are low. Natural formation of dune slacks, however, proceeds gradually. It may take many years before a beach plain is effectively cut off from the influence of the sea by enclosing dune masses or before intensive sand blowing stops when the local water table had been reached. In this way colonisation can proceed slowly through stepwise establishment of local populations. Secondly, sod cutting removes most of the existing vegetation and may also remove relic populations of endangered plant species. For this reason, parts of the mature vegetation are usually left intact.

Constructing new slacks

The creation of new slacks is, for instance, applied when sand is needed for coastal defence in order to fill in 'weak' spots in the fore dunes. Dune slacks have also been created unintentionally, sometimes as a result of the creation of sand dikes, which were intended to prevent erosion by storm floods or just to reclaim land from the sea. Some of the largest and best-developed dune slacks were 'created' in this way on the Dutch Wadden Sea islands. Sometimes new dune slacks were constructed to compensate for damage inflicted to dune slacks elsewhere (Londo, 1971; Westhoff & van Oosten, 1991).

Successful restoration projects; which ones and why

In the Netherlands, success of a restoration project is almost always judged by whether or not a restored site provides good growing conditions for rare or endangered plant or animal species. So consequently a restoration project is considered a success if many endangered species (Red List species; see Weeda et al., 1990) establish in restored slacks and can maintain large populations for at least several decades. A list of Red List species used in the present study is listed in Appendix 1.

This notion of success can be quite different from what is considered a success in other parts of the world. Parikh & Gale (1998), for instance, reported on a successful creation of a dune slack in North America where a rapid vegetation development followed after constructing a new wetland which received a considerable amount of top soil saved from a donor wetland in order to stimulate vegetation growth as soon as possible. This type of wetland restoration would be considered a failure among Dutch nature managers because the input of much organic matter would encourage a rapid establishment of fast growing species, which would prevent the establishment of endangered species of nutrient-poor habitats.

In the following, we will discuss some successful projects on the Dutch Wadden Sea islands and along the Holland and Delta coasts.

'Beach plain' on the island of Schiermonnikoog: construction of sand dike

In 1959, a sand dike was constructed in front of a large beach plain on the island of Schiermonnikoog because storm floods threatened to separate the island into two parts. This sand dike prevented daily flooding with seawater, although the area was still flooded with seawater at very high tides. The dike also prevented sand blowing toward the existing young dune ridge. Within 10 years, a wealth of Red List species which were present behind this dune ridge were lost. Although this project was designed for the purpose of coastal defence, it is discussed here as an unin-

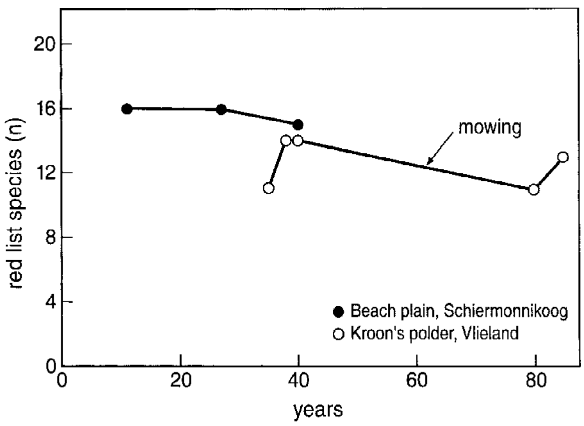

Figure 5. Changes in the number of Red List species during succession in the 1st Kroon's Polder on Vlieland and in the 'Beach Plain' on Schiermonnikoog. Both slacks were artificially isolated from the influence of the sea by the construction of sand dikes in 1910 and 1959, respectively.

tentional restoration project since new opportunities for Red List species arose behind the artificial sand dike. Between 1959 and 1977, pioneer communities of brackish environments covered many hectares. In the most western and oldest part, where groundwater discharged from the main dune body, a species rich *Schoenus nigricans* community developed with over 16 Red List species (Fig. 5), among them rare orchids, such as *Herminium monorchis, Liparis loeselii, Dactylorhiza incarnata* and *Epipactis palustris* (Van der Veen et al., 1997). Between 1977 and 1994, practically all pioneer stages of brackish and freshwater environments disappeared and were replaced by shrubs and tall grasses (Olff et al., 1993). The *Schoenus* community remained in the western part of the slack where it still covers several hectares in 1999. The stand still contains all the Red List species which were present in 1976, but their numbers have decreased considerably, while willows (*Salix repens)* and tall grasses, such as *Calamagrostis epigejos* and *Phragmites australis* have invaded the site. Since 1998 a mowing regime has been initiated in part of the slack to prevent a further loss of biodiversity.

'Kroon's Polders' on the island of Vlieland: construction of sand dike

The Kroon's Polders on the Wadden Sea Island of Vlieland have been constructed between 1908 and 1924 to prevent further sea water intrusions at the narrowest part of the island that threatened to split the island in two. Several sand dikes were built on the western beach plain of the island, which was a remnant of a former extensive dune area. Four large compartments and some smaller ones (comprising c. 200 ha), were destined for agriculture, but were never used. The enclosure by sand dikes of the first compartment of the Kroon's Polders was completed in 1911. *Schoenus nigricans* established after c. 18 years (De Vries, 1961). In the 1950s a very species rich *Schoenetum* vegetation was still present here and harboured Red List species such as *Eleocharis quinqueflora*, *Liparis loeselii*, *Epipactis palustris*, *Gymnadenia conopsea* and *Dactylorhiza incarnata.* Since then nutrient stocks increased and many small basiphilous pioneer species disappeared. Despite of the very low lime content in this part of the Kroon's Polders (0–0.2%; de Vries, 1961) no acidification occurred due to groundwater discharge from an adjoining dune area in the north. De Vries also noticed carbonate precipitation on the soil surface, a feature that was also observed in March 1998.

In 1974, the State Forestry Service decided to introduce a yearly (late August) mowing regime in the slack to restore an open vegetation structure. Since then a very stable and species-rich *Schoenetum* vegetation has been present in the slack (Fig. 5). This stability appears to be associated with very stable and high water levels.

'Meinderswaal' valley on the island of Goeree: sod removal and grazing

The Meinderswaal valley (c. 2 ha) is situated in the Middel- en Oostduinen area (200 ha) on the island Goeree. The slack is a remnant of a former beach plain, where the sea had access until 1850 and deposited calcareous sand and thin layers of clay in the slack. The adjacent dune area is used for drinking water production since 1938. These dune areas were traditionally grazed by sheep and cattle, but this practise was terminated when a new technique of drinking water production was introduced in 1955: open infiltration of eutrophic surface water from large rivers. In the late 1970s the original dune slack vegetation dominated by *Schoenus nigricans* had completely disappeared due to severe eutrophication (dumping of sludge) and replaced by reed (*Phragmites australis*) and tall forbs. Restoration of the valley has been carried out in two steps: during the winter of 1988/1989 the upper part of the valley was sod cut just down to the calcareous sandy soil, while the lower peaty part of the valley was sod cut during the winter of 1990/1991,

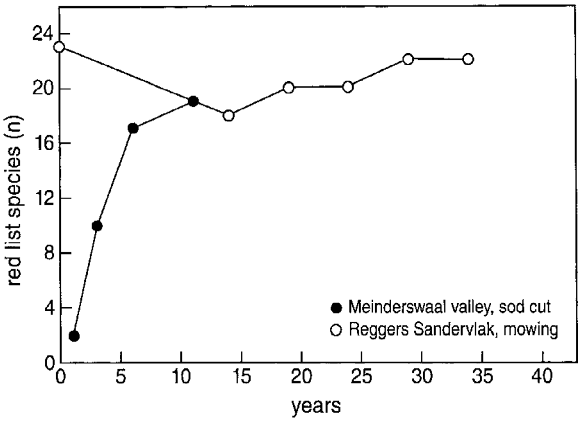

Figure 6. Changes in the number of Red List species during succession in the dune slacks with a calcareous soil (>2% $CaCO_3$) Reggers Sandervlak' and 'Meinderswaal' valley. Restoration measures were mowing and sod cutting, respectively.

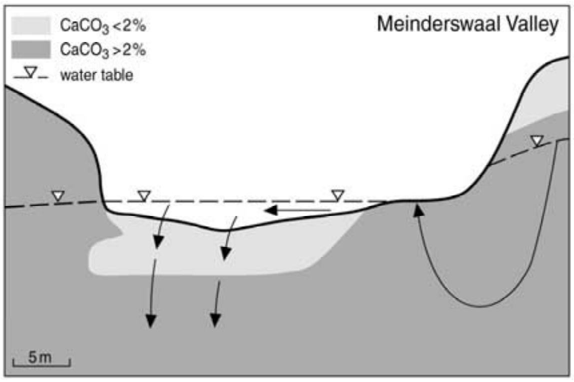

Figure 7. Hydrological system of the Meinderswaal valley (changed after Sival et al., 1997). Due to higher water levels in the upstream area calcareous groundwater is discharging in the dune slack at the right end side. This water proceeds as surface water and infiltrates again at the left end side.

but c. 1–5 cm of the organic soil remained. In 1982, sheep grazing was re-introduced in most of the dune area (c. 120 ha), including the Meinderswaal valley. In 1990, a small herd of Charolais cattle replaced the sheep, since the sheep only grazed the dry parts of the dunes, leaving the slacks untouched. Cows, however, successfully prevented a rapid spread of *Phragmites australis*, by eating the protein-rich tops. *Salix repens* and *Juncus subnodulosus*, however, were not grazed by either cattle or sheep, and gradually increased in cover.

In 1989, the vegetation of the upper part of the valley consisted of a pioneer community, in which *Anagallis tenella* established in 1990. This species was last recorded on the island in 1920. Typical dune slack species soon re-established since 1990 in both parts of the slack. The number of Red List species has increased steeply since 1990 (Fig. 6). *Schoenus nigricans*, *Dactylorhiza incarnata* and *Eleocharis quinqueflora* are now as abundant as described by Wevers (1920), but also new species established populations. *Parnassia palustris* and *Epipactis palustris*, however, did not return, probably due to lack of seeds.

The successful restoration of the Meinderswaal valley is most likely associated with the presence of an intact local hydrological system, supplying the slack with unpolluted calcareous groundwater (Sival et al., 1998). During winter, most of the valley is inundated. Infiltrated precipitation water passes through calcareous sands above a thin layer of very fine sand and seeps up along the southern edge of the valley (Fig. 7). Here, thin calcareous crusts are present on the soil surface.

'Reggers Sandervlak' North Holland Dune Reserve; hydrological measures and mowing

Reggers Sandervlak is a large secondary dune slack in the North Holland Dune Reserve situated some 150–300 m from the sea. The slack was formed about 250–300 years ago and still has a calcareous top layer due to a very high original lime content. The water tables in the slack had dropped considerably (0.2–0.5 m) due to extraction of drinking water, coastal retreat, lowering of the water tables in polder areas and by increased evapotranspiration by pine plantations. The slack became wetter after a decrease in groundwater extraction since 1976. Due to these changes in the hydrology the slack had lost many Red List species: *Dactylorhiza incarnata, Orchis morio, Gymnadenia conopsea* and *Cicendia filiformis* disappeared completely while others remained in small numbers. In the early 1980s *Hippohaë rhamnoïdes, Salix repens, Rubus caesius* and *Calamagrostis epigejos* dominated the vegetation. To prevent a further loss of Red List species a mowing regime was introduced and about 3 ha was mown every year in autumn. This mowing regime was rather successful and the populations of Red List species increased (Fig. 6). Even new red list species appeared, such as orchid species as *Dactylorhiza majalis* and *Dactylorhiza maculata*, which spread relatively easy. As a restoration technique mowing in this dune slack was efficient because most species, although threatened, were still present and the calcareous soil in this slack is well buffered against acidification.

'Moksloot' area on the island of Texel: hydrological measures and sod cutting

The Moksloot area, consisting of c. 250 ha of dunes and dune slacks, is situated at the south-western part of the island of Texel. The first vegetation descriptions of the area were made in c.1850 by Holkema (1870) who found many basiphilous pioneer and marsh communities in the largest slacks. Since then a retreat of the west-coast, the digging of a ditch (Moksloot) in 1880, drainage in nearby polder areas and, since 1956, extraction of groundwater in the slacks for drinking water purposes led to much drier conditions. Eutrophic reed beds with *Phragmites australis* and *Carex disticha* dominated the lower parts of the slacks, while the higher parts were covered by tall grasses such as *Calamagrostis epigejos* or willow shrubs (*Salix repens*). Some areas were mown in August to preserve species-rich grasslands with *Anagallis tenella, Ophioglossum vulgatum, Schoenus nigricans* and *Epipactis palustris*. After the termination of groundwater extraction in 1993, it was decided to restore the original species-rich dune slacks and top soil removal was applied in 16 slacks with a total area of over 35 ha. The depth of sod cutting varied between 10 and 40 cm.

In 1995, a small herd of Highland cattle and Exmar ponies was introduced to prevent a rapid growth of the vegetation in the sod cut areas. Only one small sand blown valley was fenced to prevent intensive trampling by cattle and horses. The vegetation development was monitored in several slacks from 1994 onwards (Grootjans et al., 2001).

Surprisingly, the species richness measured in the monitoring plots one year after sod cutting was approximately the same as in plots situated in adjoining sites that had not been sod cut. During the five years of monitoring, the species richness showed a steady increase (Fig. 8). The large slacks flooded by surface water started with a much higher diversity than the smaller and more isolated slacks directly after sod cutting. Almost 90% of the species was already present in 1994 in the largest slack. Species that contributed to the species richness belonged to plant communities ranging from dry dunes to eutrophic marshes. In some plots even species appeared which have their optimum in brackish sand beaches, which were not present in the study area before sod cutting. This rapid increase in species richness is unexpected, particularly in the isolated and fenced slack E, since no mature vegetation was left, no surface water could reach the area and grazing by cattle was prevented. Apparently other dispersal agents, such as dispersal by wind and birds or rabbits, are active as well.

The number of Red List species was very low at the start of the restoration measures, but increased rapidly in most slacks after 3–4 years (Fig. 9). In 1998, the number of Red list species and total species diversity was higher in the larger slacks with regular flooding by surface water compared to the more isolated slacks.

Apart from flooding frequencies, the hydrological regime favours the establishment of several Red List species in yet another way. Species, such as *Anagallis tenella, Schoenus nigricans* and *Potamogeton coloratus* showed a clear preference to those parts of the slack that were influenced by iron-rich groundwater. The groundwater flow pattern during early spring and its calcium concentration in the soil profile along an east west transect through three parallel dune slacks is shown in Figure 10. The central slack F receives groundwater from the adjoining slack C along it eastern shores, where pronounced precipitation of iron-hydroxides can be observed in early spring. This groundwater proceeds as surface water to infiltrate at the western shoreline and flows to the next exfiltration area of the low-lying slack (G).

These examples show that, despite the loss of most of the seed bank (c. 94% of the seed bank was lost), seed dispersal mechanisms were very effective in the area. Most of the species of the local species pool were still present nearby. Flooding in winter and early spring transported large numbers of seeds and plant fragments to the sod cut areas. Furthermore, the Moksloot area was visited by many ducks, gulls and geese, which used the sand flats as resting places. These birds may well have contributed to the rapid dispersal of many plant species that were rare or even completely absent from the area and originated from a regional species pool. The hydrological conditions had improved considerably for typical dune slacks species, due to the termination of the groundwater extraction and the rewetting of dune slacks situated upstream in the hydrological gradient. Calcareous groundwater and surface water could re-enter most slacks in spring and this has led to a higher pH in summer in most slacks (Grootjans et al., 2001).

Less successful projects; which ones and why

Because most restoration projects in the dune area have only started recently, it is difficult to judge whether they will be successful in the future. In some

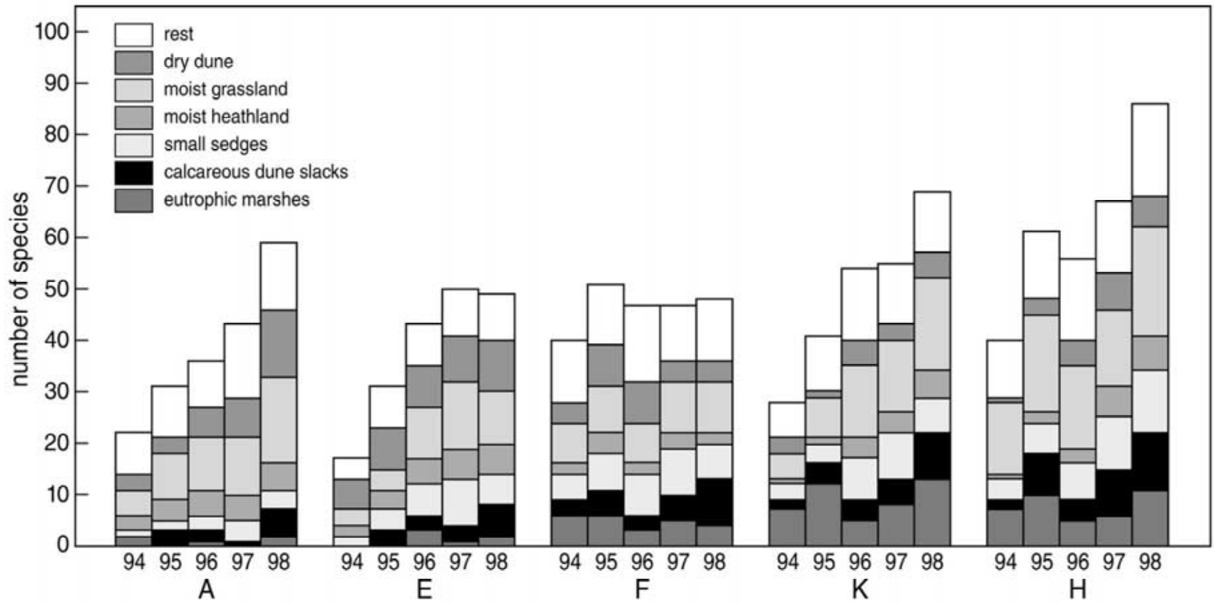

Figure 8. Changes in species-richness over 5 years, observed in 5 sod-cut dune slacks in the Moksloot area on the island of Texel (from: Grootjans et al., 2001). The changes in species-richness were measured in permanent plots of 10 × 10 m. A = isolated acidic slack, E = isolated acidic secondary slack, F = isolated calcareous through-flow slack, K and H = primary slacks flooded by surface water.

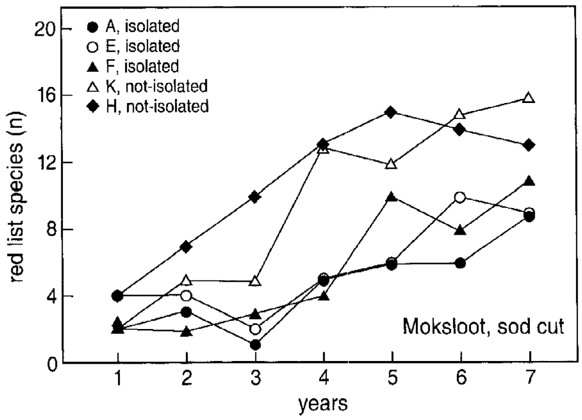

Figure 9. Changes in the number of Red List species during succession in sod-cut dune slacks in the Moksloot area, Texel (see also Fig. 8). All slacks were partly sod cut in 1993. The number of Red List species refer to the sod cut parts only (from Grootjans et al., 2001).

projects many target species established new populations shortly after the start of the project, but soon disappeared again. In other projects, almost none of the target species appeared during the first 5 years, but this might be due to a lack of seeds and such projects may become successful later. We will, therefore, classify projects as less successful if only a few of the target species established after 5 years, or when most of the target species showed a rapid decline shortly after establishment.

In the following, we will discuss some less successful projects along the Dutch coast.

'Van Hunenplak' on the island of Terschelling: creating a new dune slack

The dune slack Dodemanskisten on Terschelling (see map Fig. 1) was a natural dune slack which was once famous for its wealth of Red List species, mostly pioneer species of rather acid to neutral habitats (Holkema, 1870). These pioneer communities have existed for many decades, probably due to intensive sand blowing which prevented rapid succession (Westhoff & van Oosten, 1991). Planting of pine forests and drainage in the surroundings led to a loss of most species around 1940. Nowadays the slack is an eutrophic duck pond. To compensate for these losses a new pond had been excavated (van Hunenplak) nearby in a decalcified dune complex in 1950. This was the first example of a constructed dune slack in the history of the Netherlands. Although some target species established populations during the first 5 years (Fig. 11; *Pilularia globulifera, Cicendia filiformis, Juncus pygmaeus*, and *Littorella uniflora*), practically all species disappeared within 10 years (Sýkora, 1978). Wet heathland spe-

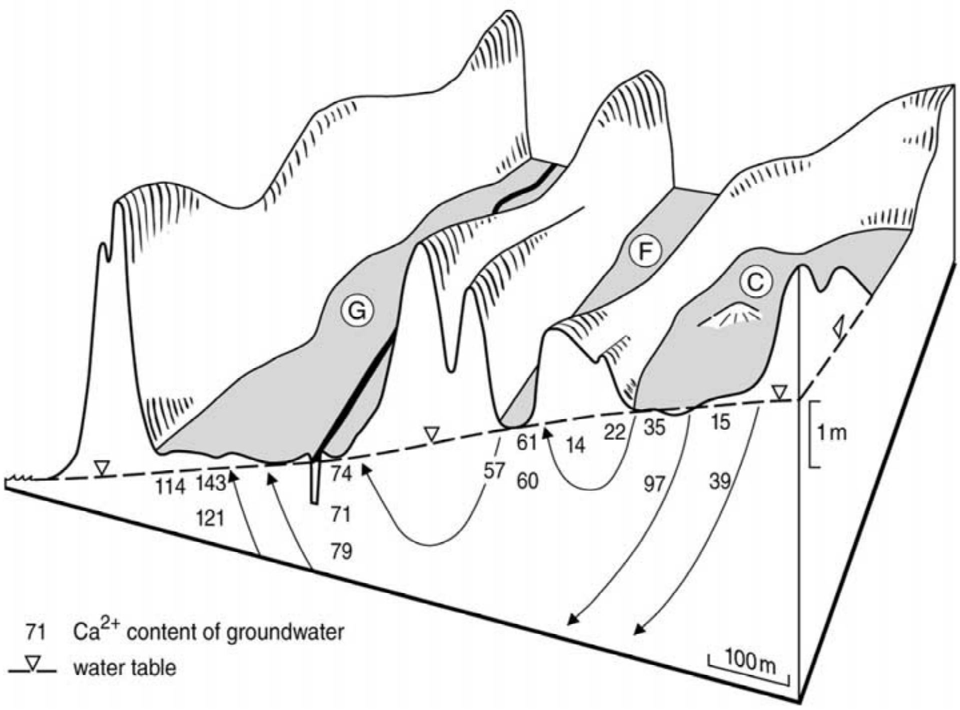

Figure 10. Hydrological system of the Moksloot area on the island of Texel (changed after Grootjans et al., 2001). The flow pattern of the groundwater has been derived from the Ca^{2+}-content of the groundwater in the soil profile. Dune slack C functions as an infiltration area and supplies dune slack F with calcareous groundwater, which infiltrates again at the western part of the slack to surface again at the eastern part of slack G. The centre of slack g is supplied with slightly brackish groundwater from deeper layers.

cies moved in quickly due to rapid acidification of the top soil. At present the pond is completely surrounded by birch wood and natural processes to counteract acidification, such as sand blowing, have become impossible.

'Vogelmeer' in the National Park Zuid Kennemerland: creating a new slack

The dune slack Vogelmeer (bird lake; see map Fig. 1) was constructed between 1951 and 1955 to compensate for the almost total loss of wet dune slack vegetation due to groundwater extraction for the public water supply and by afforestation (Londo, 1971). The vegetation development in most of the slack started in 1952. Between 1956 and 1968, vegetation development was monitored in great detail by Londo (1971). The dune slack is situated in relatively calcareous dunes along the western part of the Dutch coast (lime content 4–9%). With respect to species richness the project was successful. Between 1956 and 1959, the total number of species increased, but between 1959 and 1968 the species richness remained nearly constant at c. 170 species. The number of Red List species, however, showed a slow increase during the first 15 years (Fig. 11) and started to decline shortly afterwards, due to growth of tall grasses, sedges and shrubs. The aim to regenerate the plant community Junco baltici-Schoenetum nigricantis (Schaminée et al., 1995) failed due to decreasing water tables in the surroundings. Some characteristic species (*Dactylorhiza incarnata, Epipactis palustris* and *Schoenus nigricans)* established small populations, but they all soon disappeared. Londo (1971) compared his project with other constructed dune slacks and found that deep lakes with narrow shores were very unsuccessful in developing typical dune slack vegetation with many Red List species. Newly constructed dune slacks should resemble natural dune slacks with shallow pools and large shores. The new Vogelmeer did have such features, but yet was only moderately successful compared to natural dune slacks elsewhere. Londo concluded that dispersal problems could play a role in the early stages of succession, but the failure to develop a vegetation type with many Red List species most likely was due to unfavourable environmental conditions.

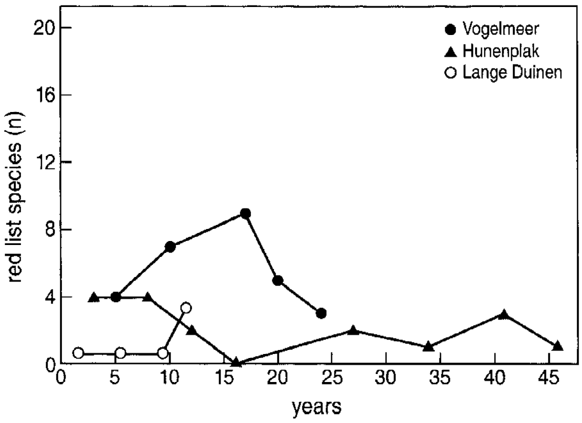

Figure 11. Changes in the number of Red List species observed in three newly created dune slacks. (Vogelmeer, Kennemerduinen; Hunenplak, Terschelling, and Lange Duinen, Ameland).

'De Lange Duinen' on the island of Ameland: creating a new slack

De Lange Duinen is a relatively young dune area on the western part of the island of Ameland. In 1989, an artificial slack was constructed behind the fore dunes to provide sand for reinforcement of some inner dune ridges. The soil was not yet completely decalcified in the newly constructed slack and hydrological research predicted some discharge of groundwater into the slack. However, the constructed shores were much too steep to produce habitats required by typical dune slack species. Furthermore, the deep excavation left little of the soil seed bank and dispersal mechanism were apparently not very effective, since only one Red List species (*Centaurium littorale*) was found in 1990. Along the deep pool surrounded by dry 'beaches' *Carex oederi* was registered in 1995 and 1997. In 1999, 10 years after the construction of the dune slack, three more Red List species appeared: *Epipactis palustris, Sagina nodosa* and *Juncus arcticus* (Fig. 11).

'Koegelwieck' on the island of Terschelling: sod cutting

The dune slack Koegelwieck is situated just behind the first coastal dunes. This large slack of c. 50 ha. was formed by intensive sand blowing in the 19th century. During a severe storm in 1915, the sea broke through and the vegetation development started anew. Between 1937 and 1948, the northern part of the slack was covered with a large stand of *Schoenus nigricans* with many Red List species (Westhoff & van Oosten, 1991). A decline of Red List species prompted the managers to remove the organic top layer in 1956. The basiphilous red List species recovered well and sod cutting was repeated in 1986, 1990 and 1995. This led to a mosaic of sod cut experiments forming a chronosequence covering almost 80 years. Vegetation and soil development has been studied annually since 1991 (Sival, 1996; Berendse et al., 1998; Lammerts, 1999). Hydrological investigations revealed that, when flooded, the slack functioned as a throughflow lake, with inflow of calcareous groundwater at the south and infiltration of mainly precipitation water in the north (Fig. 12).

Monitoring of vegetation changes in the different sod cut experiments showed that the number of Red list species increased rapidly within 8 years after sod removal and reached comparable numbers as recorded in 1948 (Fig. 12). In the site which was sod cut in 1986, the number of Red List species showed a steady decline which was associated with a rapid increase of organic material in the top soil and a decrease in pH (Berendse et al., 1998). The site which had been sod cut in 1956 and the not sod cut sites had accumulated a large amount of organic material in the soil compartment, were very acid and had few red List species in 1991. This number further declined during the 8 year observation period. The sod cut experiment of 1990 is particularly interesting since this area was excavated much deeper (10–30 cm) than the 1986 site (c. 5–10 cm). This led to the almost complete loss of the seed bank, but also to a lowering of the soil surface and, therefore, an increase in groundwater discharge into the slack. The first species to appear were practically all species occurring in the seed bank of deeper layers (10–15 cm) of the 80-year-old stage (Bekker et al., 1999). *Juncus* species as *J. articulatus* and *J.alpino-articulatus* were most abundant. Other species with a long persistent seed bank were *Samolus valerandi, Carex flacca, Littorella uniflora* and *Hydrocotyle vulgaris.* Red List species not registered in the soil seed bank, but establishing populations 3–5 years after sod cutting were *Parnassia palustris, Epipactis palustris,* and *Juncus arcticus.* No increase in organic matter could be measured after 9 years, indicating that the pioneer stage in this deeply sod cut site is more stable than in the shallow sod cut site (1986 site), where many Red List species appeared almost immediately, some in large numbers, but disappeared again within 15 years. The increased groundwater flow in the 1990 site slowed down the accumulation of organic matter. Although most of the soil seed bank had been re-

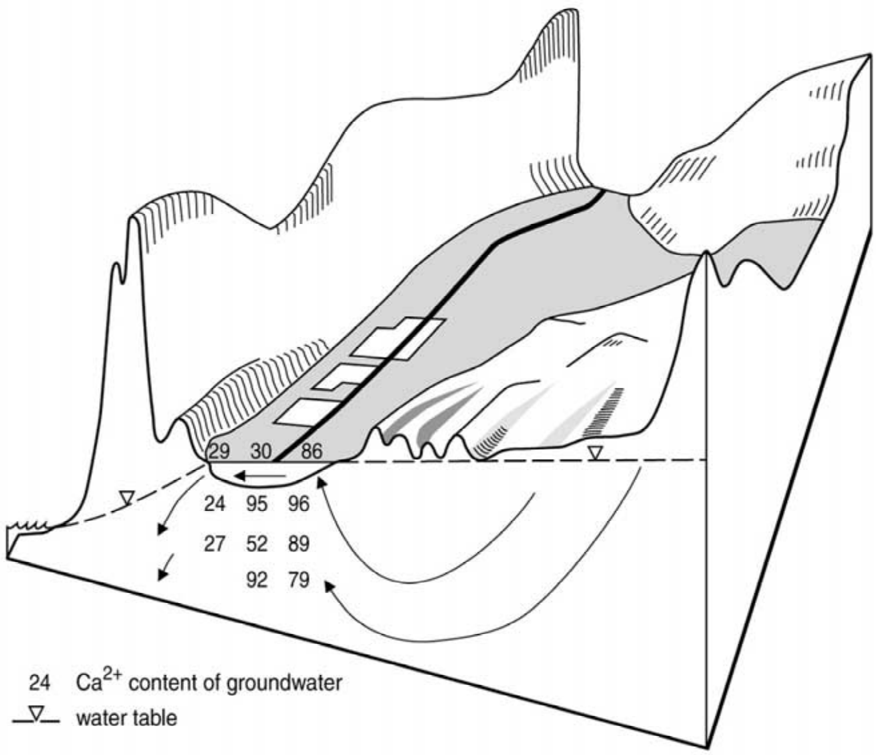

Figure 12. Hydrological system of the dune slack Koegelwieck on the island of Terschelling. Calcareous groundwater from adjoining infiltration areas discharges at the right end side of the slack. The water proceeds as surface water and is mixed with precipitation water after heavy rainfall and infiltrates again on the other side. This flow pattern of the groundwater has been derived from the calcium contents measured in both surface water and groundwater in spring 1992.

moved, dispersal mechanisms were still effective and most target species established populations within 10 years.

'Kapenglop' on the island Schiermonnikoog: hydrological measures and sod cutting

The 400-year-old primary dune slack Kapenglop on the island of Schiermonnikoog (see map Fig. 1) had lost most of its characteristic dune slack species between 1964 and 1985 (Grootjans et al., 1991), due to a number of changes in environmental conditions: (i) increase in groundwater extraction from 8 000 m^3/yr in 1950 to 150 000 m^3/yr in 1988, causing a general drop in water tables of 8–20 cm in the Kapenglop area, (ii) lowering of the water table in the southern infiltration areas, (iii) planting of pine forests to the east and the general development of shrub vegetation in the surroundings, both increasing evapotranspiration rates in the whole area. Despite a mowing regime since 1977, only three Red List species remained in 1999. In 1992, a pilot study for future restoration was carried out in the eastern part of the dune slack, which was least, influenced by the groundwater extraction. After sod-cutting almost 10 Red List species reappeared within two years, amongst them *Schoenus nigricans, Parnassia palustris, Eleocharis quinqueflora*, and *Gentianella amarella.* These species probably all emerged from the soil seed bank or from relict populations nearby. This sod-cutting experiment, however, was not very successful since all but 5 Red List species disappeared within 7 years (Fig. 13). Apparently the soil seed bank and local dispersal mechanisms were still effective but the environmental conditions were unfavourable. Hydrological research (Sival et al., 1997) showed that calcareous groundwater could reach up-gradient parts of the slack only under extremely wet conditions in early spring (Fig. 14), which occurred only in very wet years. During most of the observed period, infiltration condition prevailed, which stimulated a rapid growth of bryophytes, such as *Calliergonella cuspidatum*. In 1994, a larger part of the slack was sod-cut after the influence of groundwater extraction was reduced by transferring

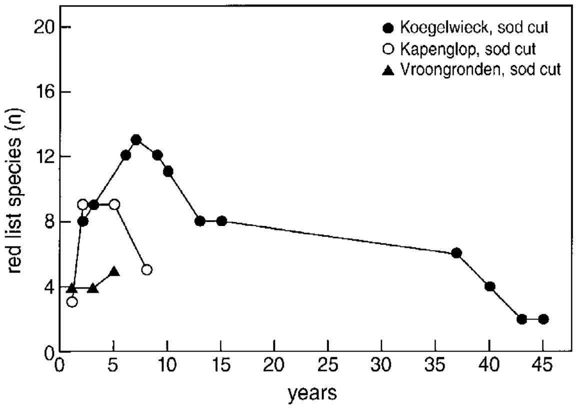

Figure 13. Changes in the number of Red List species observed in three dune slacks with a disturbed hydrological system (Koegelwieck, Terschelling; Kapenglop, Schiermonnikoog, and Vroongronden, Schouwen). The changes in the dune slack Koegelwieck were derived from sod cut experiments forming a chronosequence.

part of the production field to the western part of the island. Most Red list species appeared within 5 years. The prospects of this new restoration attempt are better since accumulation of the organic matter in the top soil is much slower in the newly sod-cut sites. At present, further improvement of the hydrological system is prevented by low water levels in the local infiltration areas of the slack. Higher water levels, however, would flood a tennis court during the winter. More adequate planning in the future could solve these problems.

'Vroongronden' on the island of Schouwen; sod cutting

A large sod-cutting project was carried out in 1994 in the dunes of the Delta coast on the island of Schouwen to restore typical dune slack vegetation types that were lost during the last three decades, due to lowered groundwater tables and increased acidification. The gently sloping dune area included a series of small dune slacks, which were flooded during wet periods and where relic populations of *Littorella uniflora, Apium inundatum, Eleocharis quinqueflora, Radiola linoides* and *Anagallis minima* had remained in only one small slack. Six other Red List species became extinct in the period between 1960 and 1985. After sod cutting *Littorella uniflora, Carex oederi, Anagallis minima* immediately established small populations in all sod-cut slacks (Fig. 14). *Radiola linoides* appeared two years later. Five years after carrying out the restoration measures, none of the other Red List species re-appeared. Detailed hydrological research showed that some of the slacks still function as 'through flow lakes'; during very wet periods precipitation water infiltrates in the whole area, which causes a pronounced raise in water tables, with highest water levels in the centre of the dune area. All dune slacks are flooded but the central ones have slightly higher (absolute) water tables compared to the slacks situated down-slope (Fig. 15). Since the slacks are not connected, a temporary cascade of water levels exists during very wet periods. Under such conditions, the up-slope slacks provide the down-slope slacks with calcareous groundwater. The groundwater has become calcareous passing through the shallow calcareous soil layers. These dune soils are relatively young and decalcification has occurred only in the top soil layers. Weather conditions from year to year have a pronounced effect on this hydrological mechanisms. But drainage ditches on both sides of the hydrological gradient have a much stronger impact. In this case, the ditch preventing flooding at the adjoining road, also prevents winter water tables to raise sufficiently to generate regular groundwater flow to the dune slacks in the centre of the dune area. Drainage in the down-slope camping site prevents regular groundwater discharge in the slacks at the lower end of the dune area. Interference with this very delicate hydrological system is probably the reason why conditions in the slacks are not optimal for Red List species. Considering the fact that only species with relic populations within the area established new populations after sod cutting, we may also assume that either seed banks of many other species were depleted or that dispersal mechanisms were ineffective.

Evaluation and restoration theory

Evaluation of case studies

Based on the case studies mentioned above, the following patterns of the restoration process in dune slacks can be observed (Fig. 16): (1) Unsuccessful projects include restoration projects where measures have been carried out in unsuitable sites; seed banks were depleted and dispersal mechanisms were not effective. Most of these projects were carried out to compensate for losses in existing nature reserves. (2) Temporary success, followed by rapid decrease of typical dune slack species can be observed in areas where seed banks were still present and dispersal mechanisms were effective, but where soil conditions and

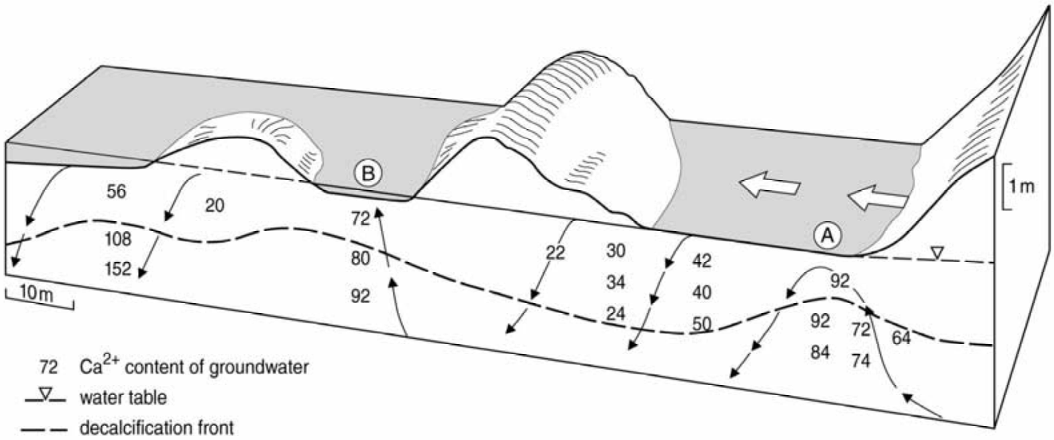

Figure 14. Hydrological system of the dune slack Kapenglop on the island of Schiermonnikoog (changed after Sival et al., 1997). The flow pattern of the groundwater has been interpreted from the calcium content of the groundwater in the soil profile and the position of the decalcification front. Calcareous groundwater enters the slack underneath the eastern slope (point A), where the decalcification front is situated high in the soil profile. The groundwater mixes with calcium-poor precipitation water at the soil surface and infiltrates again to deeper layers. In the central part of the transect (point B), groundwater discharges when the water level in the eastern slack has dropped below the surface.

hydrological regimes were sub-optimal. Examples are fresh water slacks surrounded by decalcified dune areas, where many changes in the hydrological regime had occurred. (3) Successful reconstruction of dune slacks in areas with hydrological systems that were little influenced by man and where dispersal mechanisms were effective. Pioneer stages, however, were relatively short lived. A good example is the Koegelwieck on the island of Terschelling. (4) Very successful projects where many typical dune slack species established in large numbers and persisted for many decades. These examples include the large sandy beaches on the Wadden Sea islands, which were enclosed by artificial dikes of drift sand. Local and regional species pools were available and dispersion mechanisms were still effective. Successful projects also include some examples in which a traditional management was re-installed. Good examples are Meinderswaal valley and Reggers Sandervlak situated in the calcareous dune areas of the mainland coast.

Analysing the restoration process further, we can distinguish three different environmental conditions influencing the stability and recovery process of young dune slack ecosystems. These conditions are most favourable when the soil is nutrient-poor and well-buffered (pH > 6), prolonged flooding with base-rich groundwater occurs and when the soil remains moist during dry summers. The latter condition is usually only fulfilled when the slack receives an additional flow of calcareous groundwater from adjoining dune areas. Under such conditions the accumulation of organic matter is slow (Fig. 17a). Nutrient-poor conditions and flooding in spring prevent the establishment of very productive species, while base-rich conditions stimulate the mineralisation of organic matter production of the pioneer species, keeping the nutrient stocks low. The best results are obtained in large beach plains that have been partly embanked by artificial sand dikes. Vegetation development (stage 1) starts under near natural conditions here. Usually the typical dune slack species can easily colonise such areas since small populations are practically always present in older stages nearby, and dispersal mechanism (wind, water, animals) appear to be very effective. If a well developed soil seed bank is present (stage 1a) the pioneer stages are rich in Red List species immediately after the restoration measures. Typical dune slack communities (stage 2) are maintained for a long time due to regular sand blowing which often starts the succession anew. Seepage slacks with a regular supply of anaerobic calcareous groundwater can also maintain pioneer stages for many decades, even when the dunes are fixed and no sand blowing occurs. It is still unclear which mechanisms are responsible for such 'stable states'. Late successional stages with grasses and shrubs may also harbour many Red List species (stage 3), but soon change into tall and very species-poor stands (stage 4). Accumulated nutrient stocks in the soil compartment appears to act as a threshold here

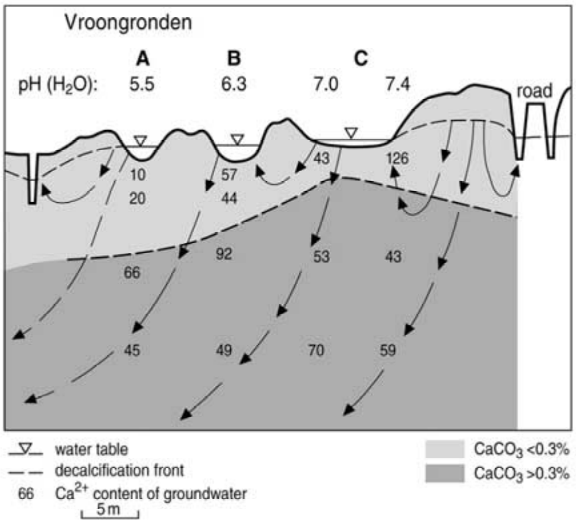

Figure 15. Hydrological system of the Vroongronden on the island of Schouwen with groundwater flow pattern derived from calcium contents of the groundwater and the position of the decalcification front in the soil profile. Also indicated is the pH of the top soil (0–10 cm) in various slacks. The infiltration area is situated close to a road, which is flanked by two drainage ditches. Precipitation passes through the calcareous sand deposits at c. 50 cm below the surface. Part of the calcareous groundwater enters slack C the eastern slope, where very high values of calcium were measured in the topsoil, possibly as a result of dissolution of secondary carbonate deposits. The decalcification front is situated high in the profile underneath the whole slack. The groundwater mixes with calcium-poor precipitation water at the soil surface and infiltrates again to deeper layers. Slack B is also supplied with calcareous groundwater from slack C. In slack A infiltration of precipitation water prevails.

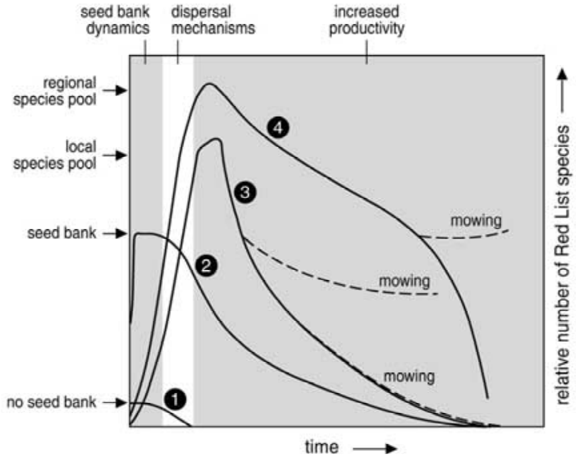

Figure 16. Conceptual model of occurrence of endangered dune slack species (Red List species) after restoration measures have been carried out. 1 = unsuccessful projects where measures have been carried out in unsuitable sites and where seed banks are depleted. 2= temporary success, followed by rapid decrease of target species is encountered in slacks where environmental conditions are unfavourable, but where seed banks are still present. 3 = successful, but short-lived, reconstruction of pioneer vegetation with many Red List species. Dispersal mechanisms are effective, but environmental conditions are sub-optimal. Mowing may sometimes retard a rapid spread of later successional species and a rapid decline in Red List species. 4 = very successful projects where many typical dune slack species establish in large numbers and persist for many decades. Natural processes retard the succession towards late successional stages. A mowing regime may stabilise the pioneer stage even longer.

(compare Hobbs & Norton, 1996), preventing further establishment of Red List species. The soil seed bank underneath such late successional stages may be still rich in Red List species (4a), but when time passes, the soil seed bank becomes depleted.

Less favourable conditions exist when a rapid acidification of the top layer occurs during succession. The result is a much faster accumulation of organic matter (Fig. 17b) and a general increase in productivity of the ecosystem (Gerlach et al., 1994). Pioneer stages after restoration measures, such as sod cutting, usually do not last long (10–15 years). If seed banks have been depleted and dispersal mechanisms are ineffective, the results of restoration measures in such areas are often very disappointing.

When the availability of nutrients in newly created slacks is high during the first successional stages, or when natural slacks have been polluted, fast growing plants species, such as *Phragmites australis*, *Calamagrostis epigejos,* or even *Urtica dioica* (van Dijk & Grootjans, 1993) can establish almost immediately and effectively store nutrients in living and dead material. The period for establishment of slow-growing pioneer species is often so short that conditions for them have become unfavourable even before most of the species have reached the area (Fig. 17c).

Restoration prospects and gaps in knowledge

Failures of restoration projects are often caused by not implementing existing knowledge or by selecting sites that cannot be expected to produce good results. Sometimes restoration measures are carried out in areas that are available, not because they are the best suitable sites for restoration of species-rich dune slacks. Existing ecological and hydrological knowledge is often good enough to estimate the success of planned restoration projects, but such knowledge is not always used, because of the costs of implementing such knowledge.

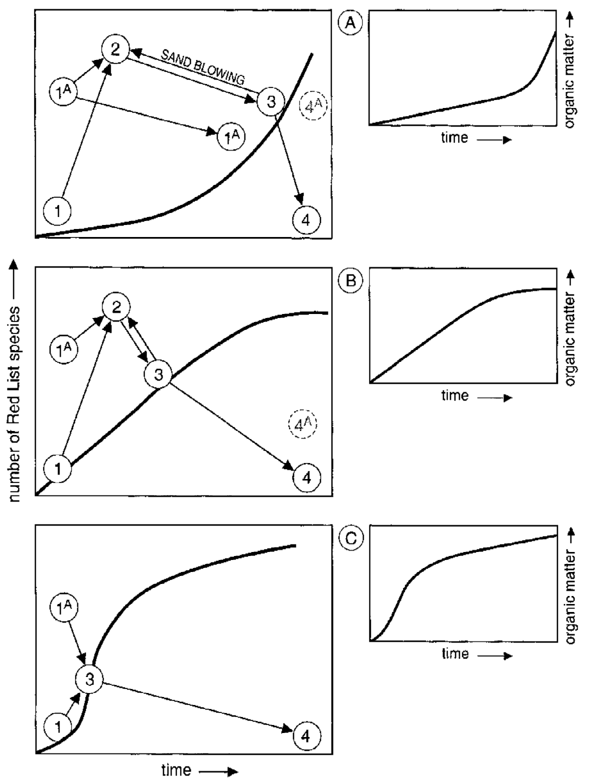

Figure 17. The rate of organic matter accumulation appears to be a threshold for a successful restoration of typical dune slack vegetation with many Red List species. When the soil is nutrient-poor, well buffered, and fed by base-rich ground water, the accumulation of organic matter is slow (Fig. 17a). Typical dune slack communities (stage 2 = target community) develop from species-rich pioneer stages (stage 1a), if a well-developed soil seed bank is available at the site immediately after restoration. If dispersal mechanisms are effective the target community may also develop from species-poor pioneer stages. Once established the target community can be maintained for a long time by regular sand blowing, which prevents a rapid accumulation of organic matter. Late successional stages with grasses and shrubs may also harbour many Red List species (stage 3), but soon change into tall and very species-poor stands (stage 4). Restoration of the target community is relatively easy, since many target species have survived in the seed bank or as relic populations in the late successional stages. Target communities with many Red List species are very short-lived when the accumulation of organic matter in soil or vegetation is rapid (Fig. 17b). The target community cannot develop if the accumulation of organic matter is very fast due to unfavourable environmental conditions. Some of the Red List species can occur temporarily in pioneer or later successional stages, but they will soon disappear. Restoration will not succeed when late-successional stages have existed for a long time and soil seed banks of the target community have been depleted.

When restoration goals are only formulated on the species level, it does not really matter in which type of ecosystems their populations are being restored. Many endangered dune slack species grow well in a large variety of dune slack types (Lammerts et al., 1999). Some species occur in large numbers in artificially created primary dune slacks, the same species can also be maintained in old secondary slacks on calcareous substrates by a mowing regime. Restoration projects are considered successful if large numbers of endangered Red List species have established new populations or if relic population increase in numbers. Such goals are formulated by most nature conservation organisations and they have broad political backing. Politicians, however, want quick results and creating new pioneer stages in existing dune slacks where relic populations are still present is often very successful during a short period. Such type of restoration often triggers comments as “gardening with wild species in natural mosaics” (Allan & Hoekstra, 1992), and the Dutch nature conservancy is well trained in such activities. The range of natural variability of ecological key parameters is well known in the case of dune slack ecosystems (Lammerts et al., 1999); it can be easily assessed whether such key parameters are outside the limits of required conditions, and it is well known which sites are best suited for optimal results. Such societal desires may, however, change (Allen, 1994) and the concept of ‘wilderness’ may become more popular. In the latter concept the method (i.e. no management measures) is often better specified than the goal, and this may conflict with a more traditional goal of preserving endangered species and landscapes. For recovery of natural ecosystems along the coast, a landscape-ecological approach (Naveh, 1994) is required. In the case of dune slacks, we need to specify natural references, identify the natural processes that form and sustain these ecosystems. Particularly important is to identify ecological and geomorphological mechanisms that create (semi-) stable states in pioneer communities, in which endangered species can survive for a long time without human interference. In our case, a reference could be the natural ecosystem formed by dynamic processes by wind and water. We have some information on what such references look like, but we have little information on dispersal strategies of endangered plant species, and how they establish populations in an increasingly unstable coastal area, e.g. connected to sea-level rise (Noest, 1991). For the Netherlands, a sea-level rise of 50–60 cm is expected over the next 100 years (van den Bergh & Nijkamp, 1998), which will no doubt lead to land losses in coastal areas that are not protected by firm dikes. However, the new government policy of ‘dynamic preservation’ of the Dutch coast also offers new possibilities to enhance nature conservation values in newly formed dune areas. This coastal defence policy primarily aims at ensuring safety against flooding and sustainable preservation of values and interests attached to dunes and beaches (de Ruig, 1998). A method to carry out this policy is 'sand nourishment' in places where sand is most needed. In a country that spends nearly 30 million USD a year on sand nourishment (de Ruig, 1998), the statement 'restoring the natural ecosystem' is not necessarily a vague statement, because such activities could stimulate the natural formation of dunes, dune slacks and even salt marshes. Creating a natural dune slack ecosystem is not an unachievable goal (Hobbs & Norton, 1996) in the Netherlands. Besides knowledge on ecological and geomorphological processes creating or sustaining such ecosystems, we need to formulate societal strategies to prevent human interventions in areas where these ecosystems can develop.

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Appendix 1. Red list species used in the evaluation of restoration projects in Dutch dune slacks

Plant community	Red List species	Plant community	Red List species
Potamion graminae	*Potamogeton gramineus*	Caricion davallianae	*Parnassia palustris*
	Potamogeton coloratus		*Juncus arcticus*
	Potamogeton polygonifolius		*Carex oederi*
Littorellion uniflorae	*Littorella uniflora*		*Anagallis tenella*
	Echinodorus ranunculoides		*Dactylorhiza incarnata*
Hydrocotylo-Baldellion	*Eleocharis multicaulis*		*Eleocharis quinqueflora*
	Deschampsia setacea		*Epipactis palustris*
	Pilularia globulifera		*Equisetum variegatum*
	Apium inundatum		*Gentianella amarella*
Saginion maritimae	*Centaurium littorale*		*Gentianella campestris*
	Sagina nodosa		*Herminium monorchis*
	Gnafalium luteo-album		*Liparis loeselii*
Nanocyperion flavescentis	*Juncus capitatus*		*Schoenus nigricans*
	Cicendia filiformis		*Pedicularis palustris*
	Anagallis minima		*Gymnodenia conopsea*
	Radiola linoides		*Linum catharticum*
	Juncus pygmeus	Nardo-Galion saxatilis	*Antennaria dioica*
	Hypericum humifusum		*Botrychium lunaria*
Armerion maritimae	*Oenanthe lachenalli*		*Platanthera bifolia*
	Odontites vernus		*Polygala vulgaris*
	Centaurium pulchellum		*Carex caryophyllea*
	Scirpus rufus		*Hypericum pulchrum*
Junco-Molinion	*Cirsium dissectum*		*Pedicularis sylvatica*
	Carex pulicaris		*Gentiana pneumonanthe*
Ericion tetralicis	*Lycopodium inundatum*	Other communities	*Cladium mariscus*
	Dactylorhiza maculata		*Dactylorhiza majalis*
Empetrion nigri	*Genista tinctoria*		*Scirpus cariciformis*
	Pyrola rotundifolia		*Rhinanthus minor*
	Pyrola minor		*Anthyllis vulneraria*
			Briza media